Chapter 1

AN ATLAS OF PHANEROZOIC CLADE DIVERSITY DIAGRAMS

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Clade diversity diagrams are spindle-shaped graphs that summarize patterns of taxonomic evolution within higher taxa through geologic time. Most clade diversity diagrams are constructed about a central axis that represents time (scaled either metrically or ordinally, by stratigraphic interval). Some measure or estimate of taxonomic diversity (or "richness") is then plotted symmetrically about the axis to give the diagram an overall spindle shape (e.g., Figure 1).

Diversity diagrams for individual clades convey information about their size, shape, and variability in the fossil record (cf. Gould et al., 1977). Such "morphologic" information is valuable for assessing how evolutionary rates (that is, rates of origination and extinction) vary within the taxa through geologic time. Clade diversity diagrams for groups of higher taxa hypothesized to be related by phylogeny or by function are useful for comparisons of the histories of the taxa. Common patterns of expansion or contraction may relate to general factors governing all taxa, whereas reciprocal patterns may be interpretable as negative interactions between pairs of ecologically similar taxa (e.g., Simpson, 1953; Bambach, this volume). Sets of clade diversity diagrams also are useful for summarizing variation among large numbers of clades for the purpose of testing general macroevolutionary models (e.g., Raup et al., 1973; Gould et al., 1977).

Phanerozoic Diversity Patterns:
Profiles in Macroevolution

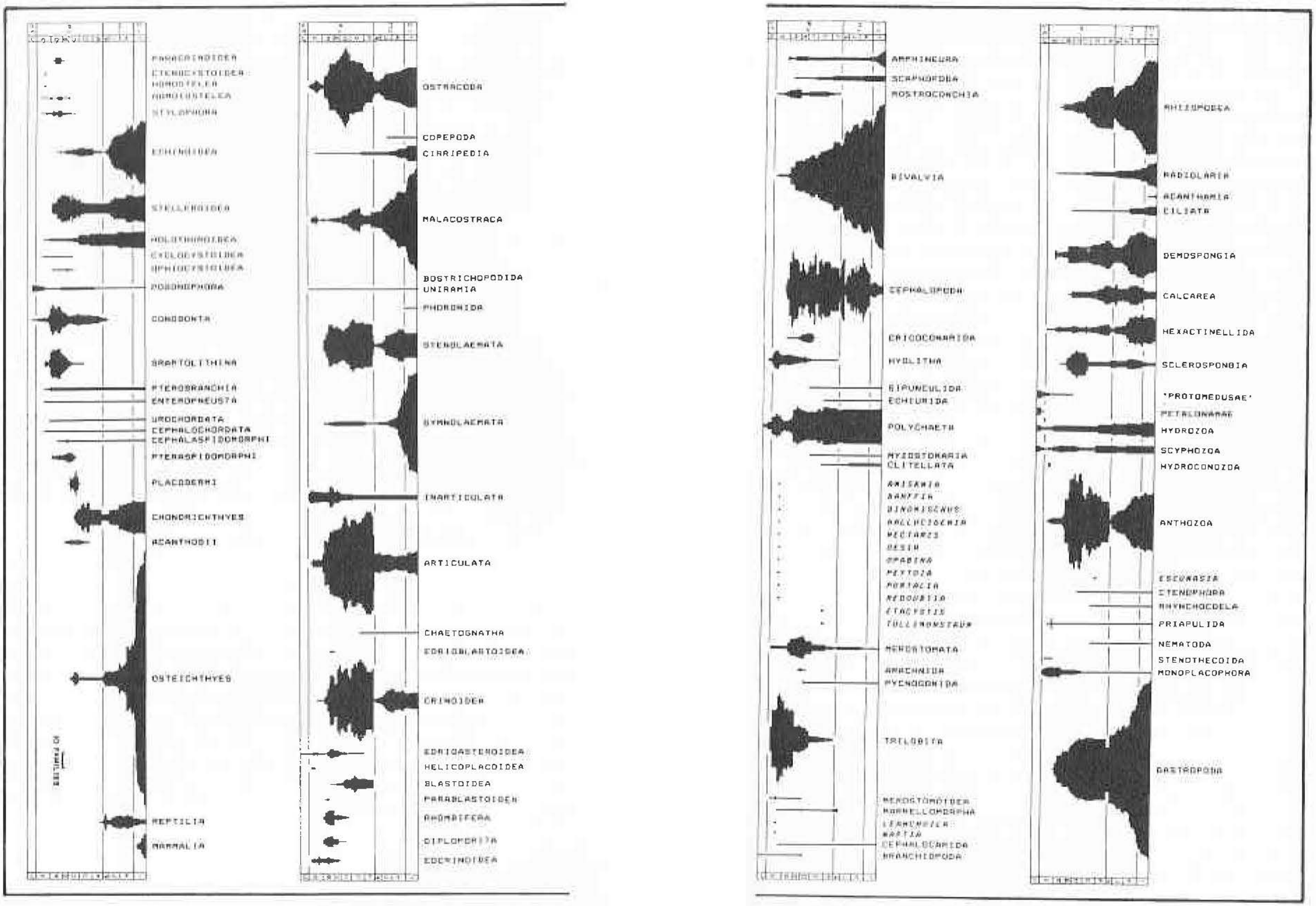


Figure 1. Families within classes of fossil marine mammals.

This chapter presents a collection of clade diversity diagrams which we hope will be useful for examining the general histories of a wide variety of animal taxa. The main body of the chapter is a series of 12 figures displaying spindle diagrams for orders, classes, and phyla of both marine and nonmarine (or "continental") animals for the whole of the Phanerozoic (including the Vendian). Nearly all of the diagrams are plotted at a uniform taxonomic and temporal resolution, specifically that of familial diversity per stratigraphic stage. The taxonomic rank of family is used simply because comprehensive data with good stratigraphic resolution can be obtained for all animal groups at this level. Although families do not display all of the detail of the fossil record, they should be sufficiently sensitive to show major evolutionary trends and patterns with characteristic timescales of fives to tens of million years (see also Sepkoski, 1979, 1982a; Raup and Sepkoski, 1982).

The clade diversity diagrams in most of the figures are formatted in strips that have time in the vertical dimension. Most of the strips are scaled from 625 myr at their bottoms to approximately 1 myr BP at their tops. (No data on Recent diversity are directly included in the diagrams.) Geologic eras and systems are indicated at the lefthand ends of the strips, with eras denoted by *Cz* = Cenozoic, *Mz* = Mesozoic, *Pz* = Paleozoic, and *pє* = latest Precambrian; systems are denoted by standard symbols, with *V* = Vendian. The widths of the clade diversity diagrams in each strip indicate the numbers of families known from direct fossil evidence or from interpolation between known occurrences to be present in the "clades" in each of 80 stratigraphic stages or comparable intervals (see Table 1 in Sepkoski, 1982b for a listing of the stages used). A scale for the familial diversities appears in the lower righthand part of most of the figures. All of the diagrams were produced with an IBM Personal Computer and Epson dot-matrix printer.

The first two figures in this chapter contain class-level summaries of the entire Phanerozoic fossil record. Figure 1 displays clade diversity diagrams for the 87 classes and 15 unique, problematic genera that have representatives in the marine fossil record. This illustration is an updated version of Figure 1 in Sepkoski (1981) with corrections based on new data in Sepkoski (1982b). The second figure in this chapter summarizes the continental fossil record. The diversity diagrams display numbers of freshwater and terrestrial families within the 39 animal classes known from the nonmarine fossil record; data on the classes were compiled from the literature sources listed in Table 1. Also shown at the bottom of Figure 2 are clade diversity diagrams for numbers of *species* within the 13 taxonomic divisions of the tracheophytes and bryophytes; the data for these diagrams were taken from Niklas, Tiffney and Knoll (this volume).

The next eight figures illustrate a breakdown of the class-level clades into their constituent orders. Time and diversity in all diagrams are plotted at the

TABLE 1. Principal literature sources of information on the taxonomy and stratigraphy of continental animal families.

Taxon	*References*
MOLLUSCA:	Davies (1971), Henderson (1935), Moore, Teichert, and Robison (1953-1982), Orlov (1958-1964), Solem and Yochelson (1979), Taylor and Sohi (1962).
ARTHROPODA: (excl. insects)	Cooper (1964), Harland et al. (1967), Kukalová-Peck (1973), Moore, Teichert, and Robison (1953-1982), Morris (1979), Mundel (1979), Orlov (1958-1964), Piveteau (1952-1969), Rolfe et al. (1983), Schram (1969), Schram and Schram (1979).
INSECTA:	Barthel (1978), Bode (1953), Burnham (1978), Carpenter (1976, 1979, 1980), Evans (1956), Grande (1980), Harland et al. (1967), Hoganson and Ashworth (1982), Jarzembowski (1980), Kukalová (1966, 1969), Kukalová-Peck (1973, 1975), MacLeod (1970), Muller (1963-1970), Orlov (1958-1964), Piveteau (1952-1969), Rodendorf (1968), Rolfe et al. (1983), Whalley (1980), Wighton (1982), Wilson (1978).
CHORDATA:	Brodkorb (1967, 1971, 1978), Carroll (1977), Charig et al. (1976), Denison (1978, 1979), Eisenberg (1981), Estes (1981), Grande (1980), Harland et al. (1967), Kuhn (1969), Lillegraven et al. (1979), Mlynarski (1976), Moy-Thomas and Miles (1971), Nelson (1976), Olsen and Galton (1977), Orlov (1958-1964), Romer (1966), Russell (1975), Steel (1970, 1973), Zangerl (1981).
OTHERS:	Clark (1969), Conway Morris (1981), Conway Morris et al. (1982), Harland et al. (1967), Kukalová-Peck (1973), Moore, Teichert and Robison (1953-1982), Schram (1979), Southcott and Lange (1971), Thompson and Jones (1980).

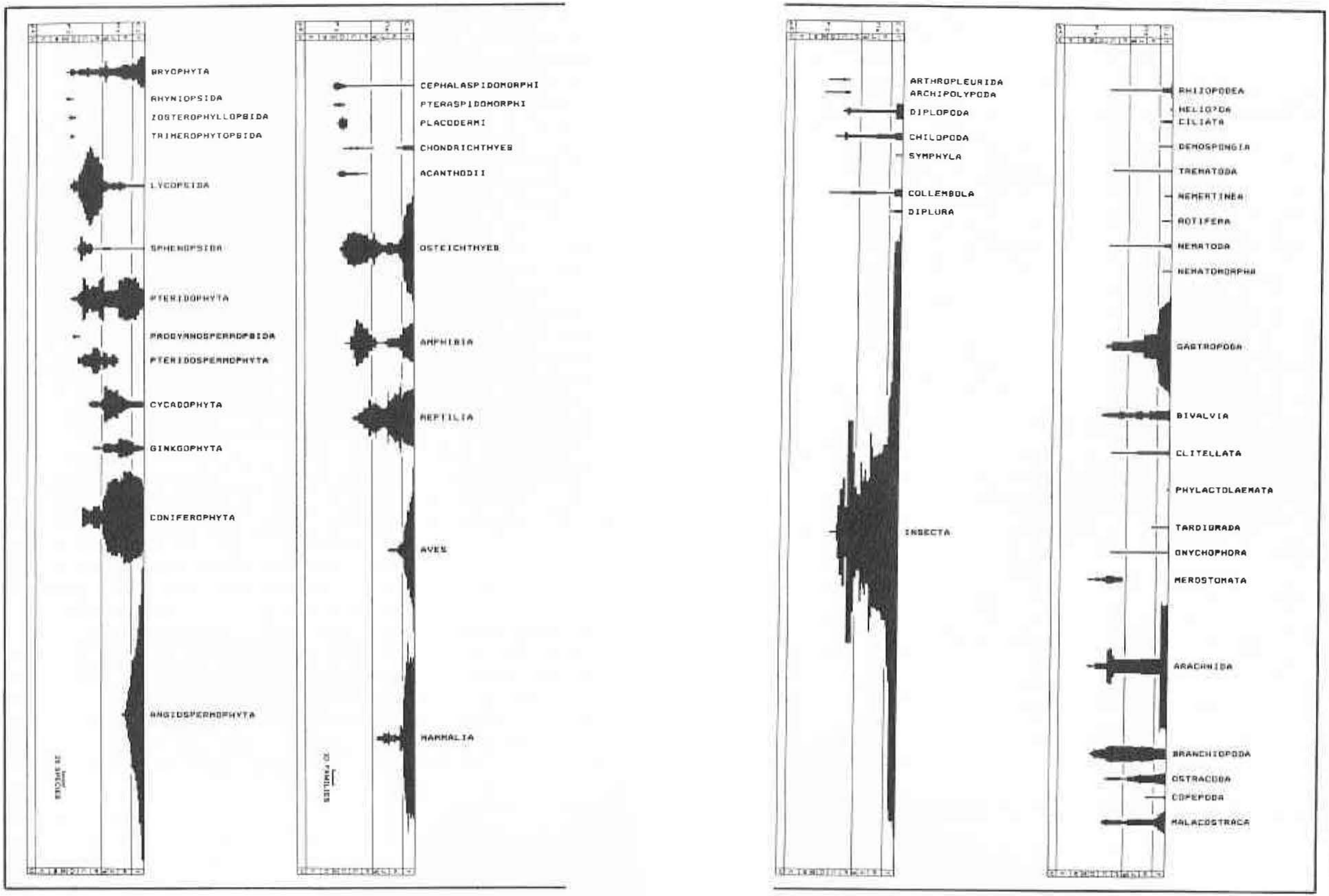


Figure 2. Families within classes of continental (i.e. terrestrial and freshwater) fossil animals and species within divisions of continental plants.

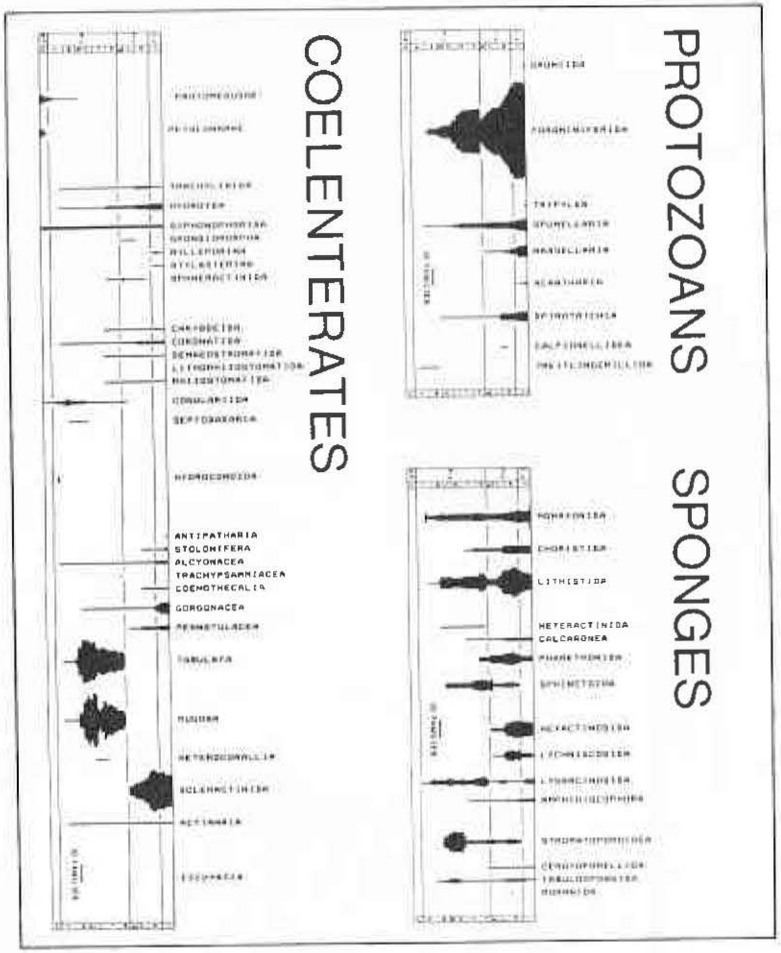


Figure 3. Families within orders of fossil "Protozoa," Porifera, and Coelenterata.

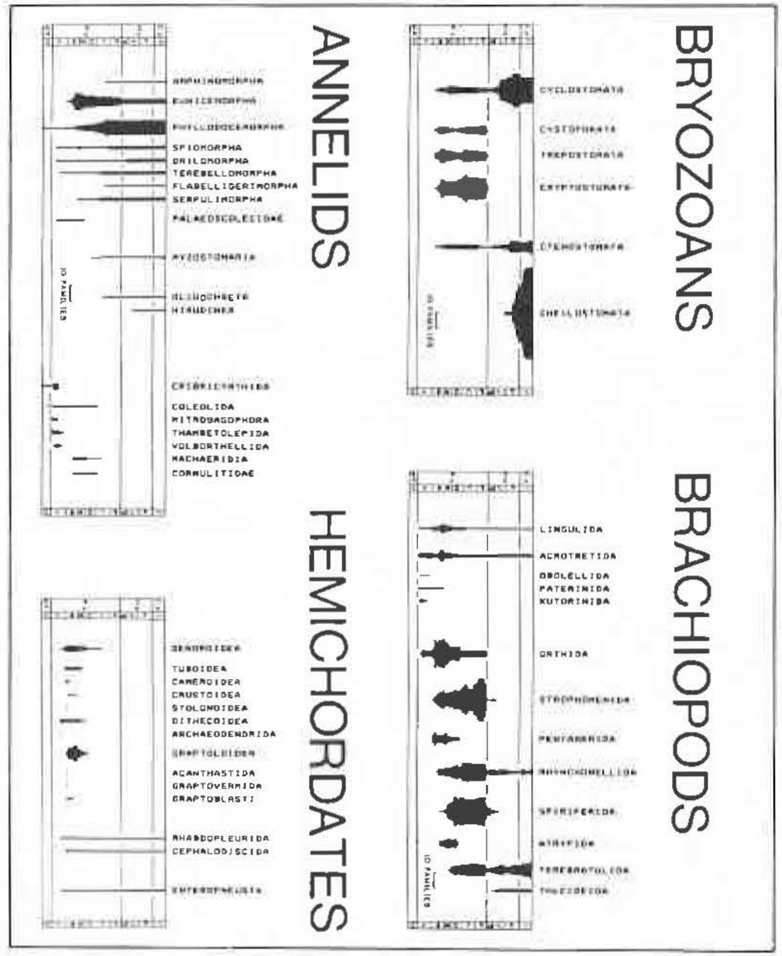


Figure 4. Families within orders of fossil Bryozoa, Brachiopoda, Annelida, and Hemichordata.

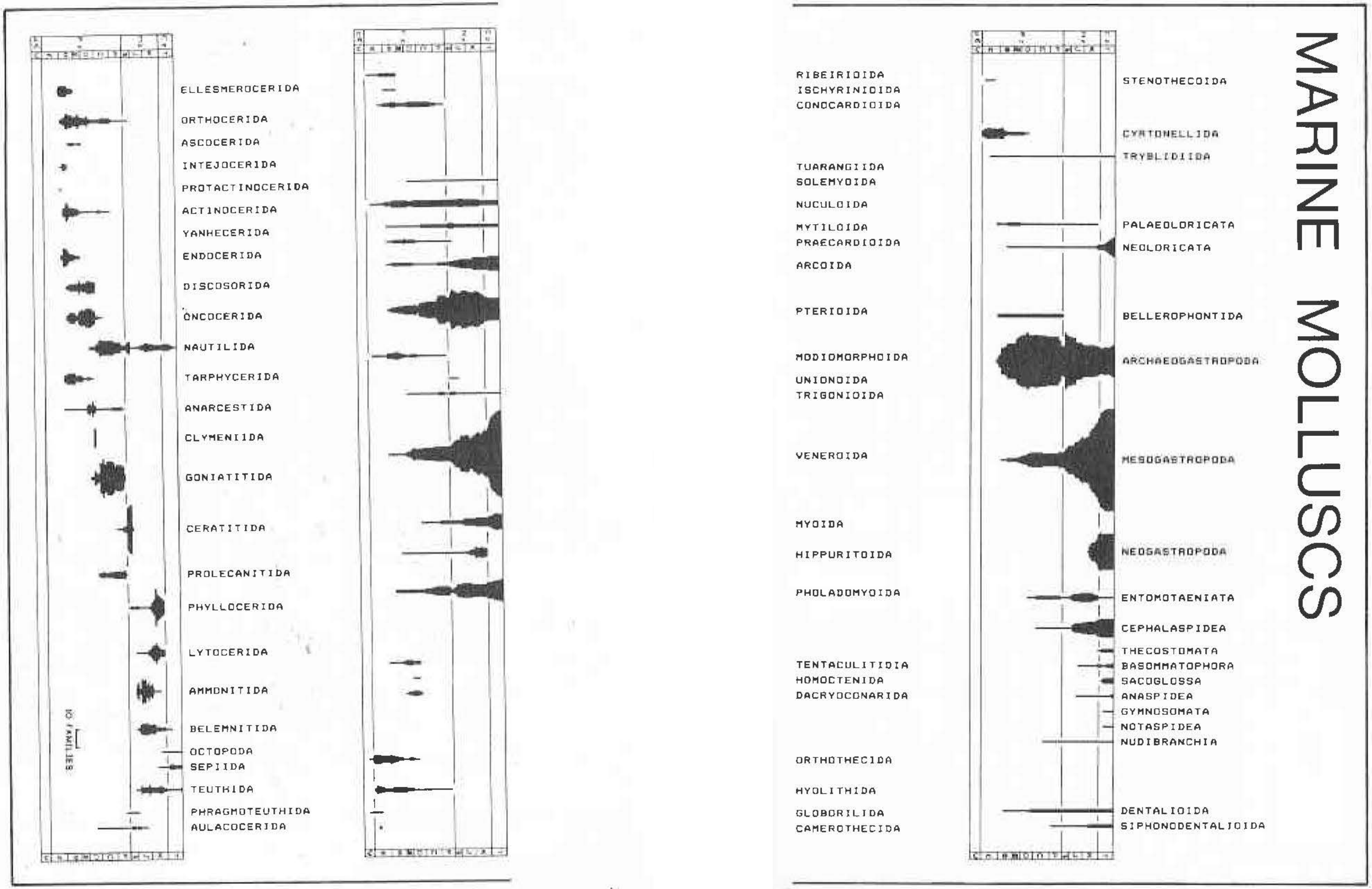


Figure 5. Families within orders of fossil marine Mollusca.

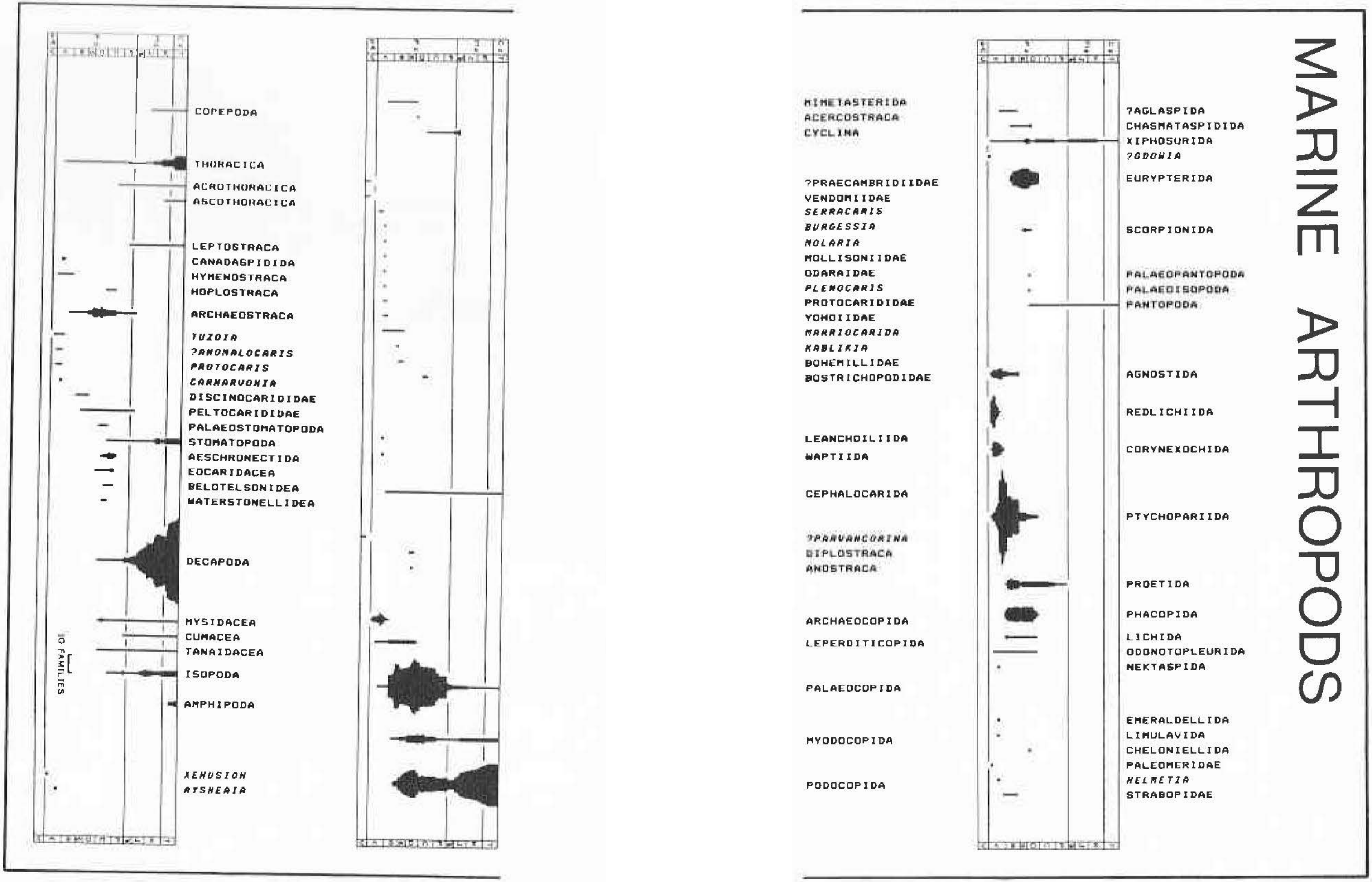


Figure 6. Families within orders of fossil marine Arthropoda.

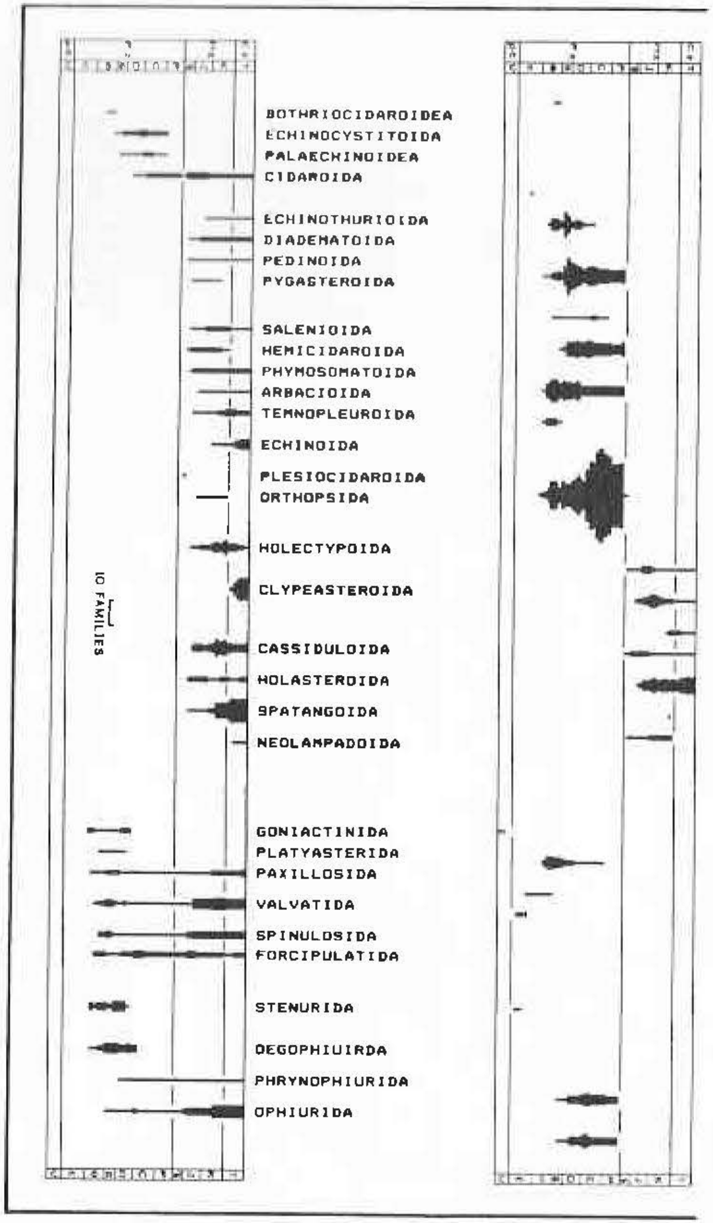
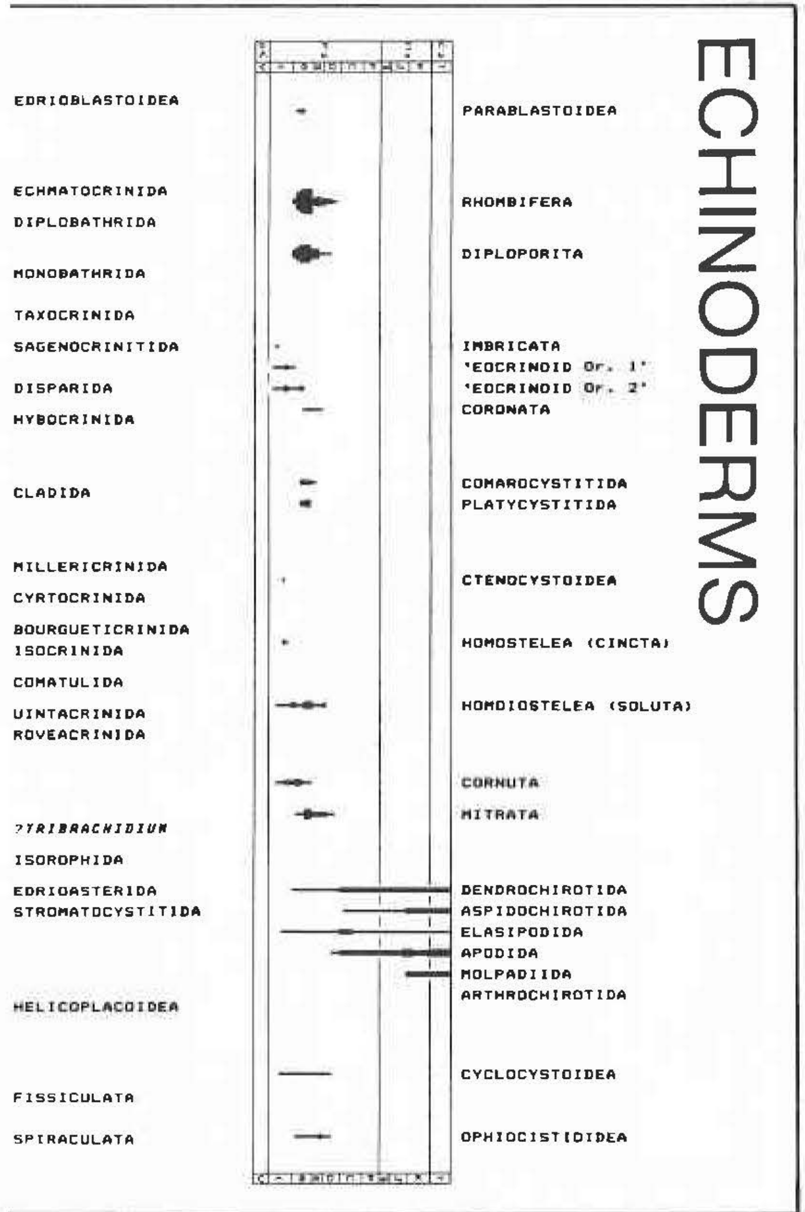


Figure 7. Families within orders of fossil Echinodermata.



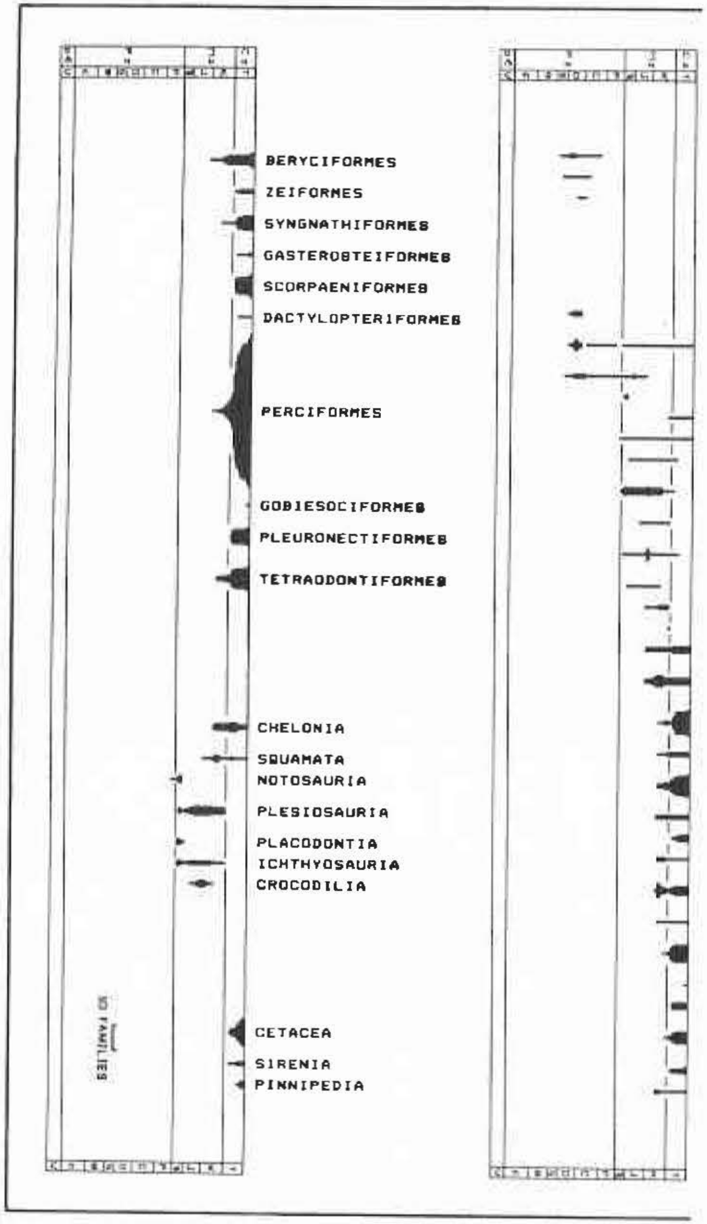
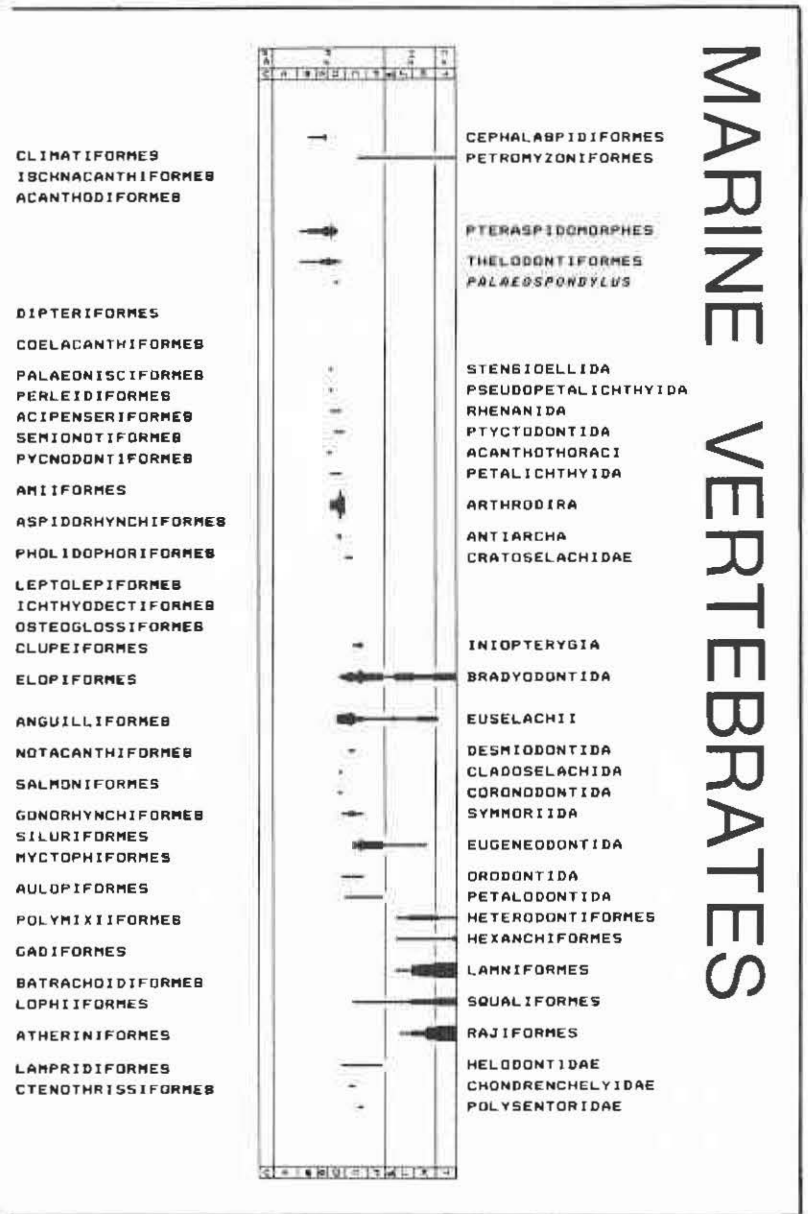


Figure 8. Families within orders of marine Vertebrata.



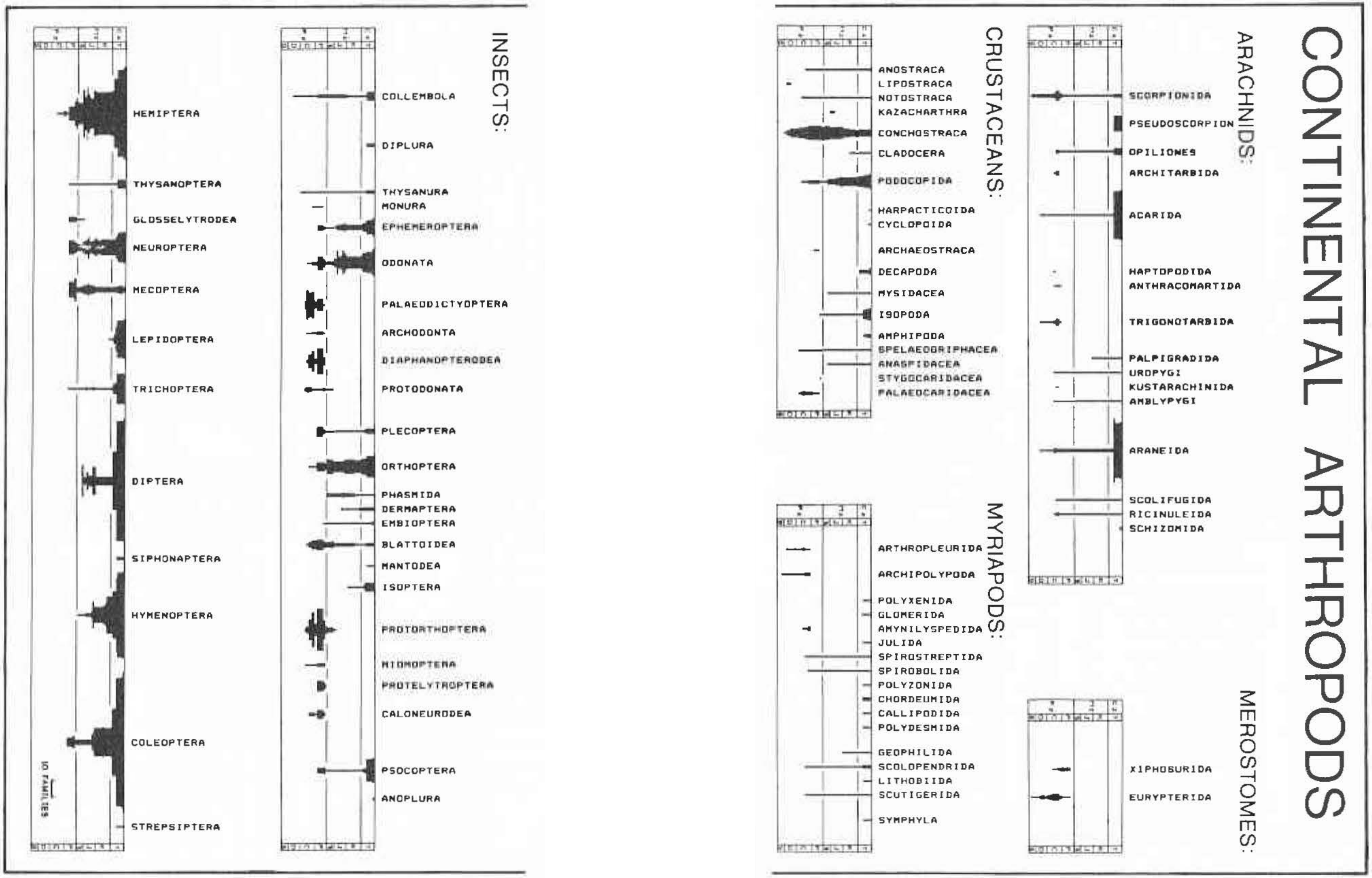


Figure 9. Families within orders of fossil nonmarine Arthropoda.

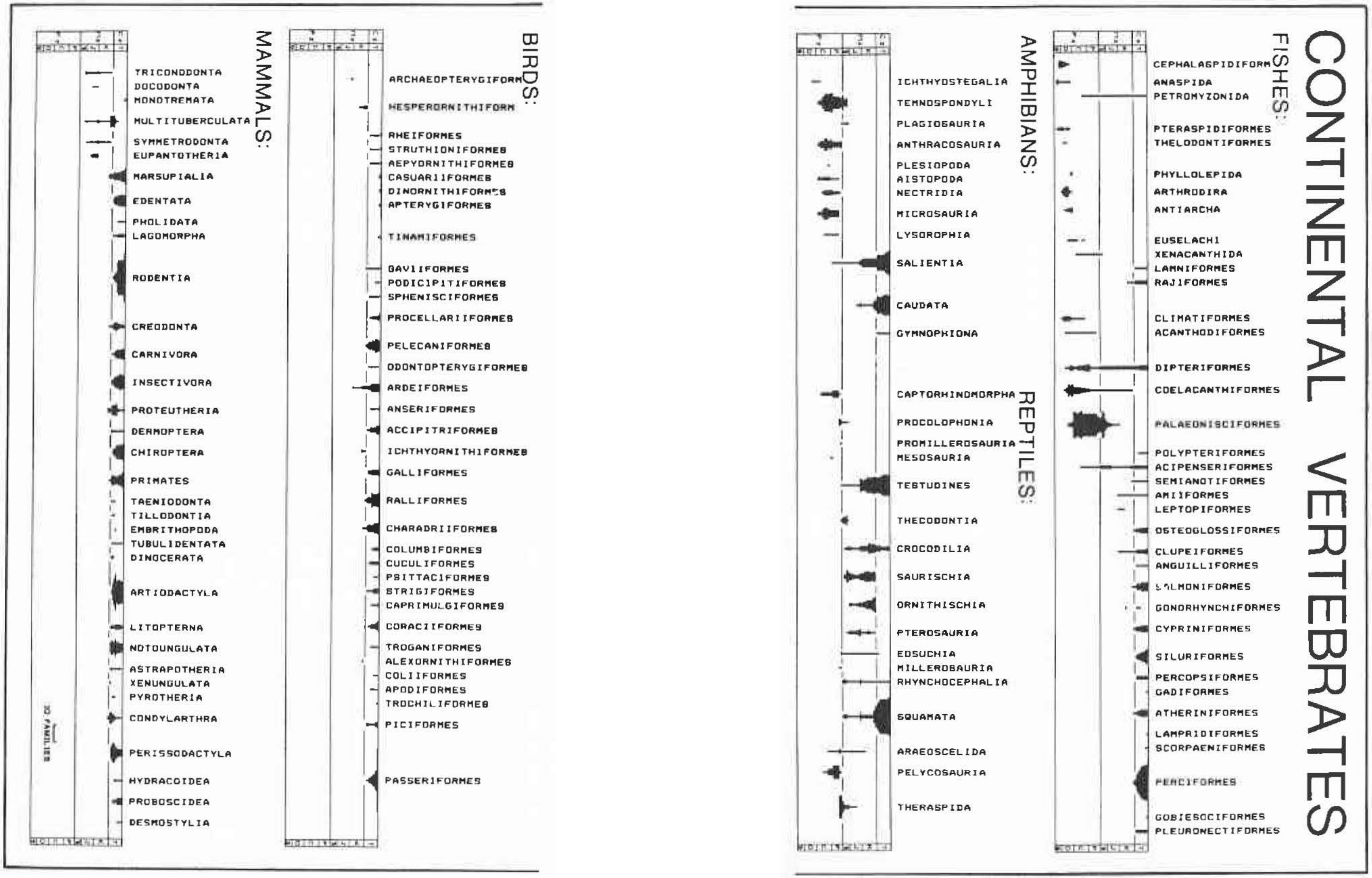


Figure 10. Families within orders of fossil nonmarine Vertebrata.

same relative scale as in Figures 1 and 2 in order to facilitate comparison. Figures 3 and 4 display family-level clade diagrams for orders within the moderately diverse marine phyla: the Protozoa, Porifera, Coelenterata, Bryozoa, Brachiopoda, Annelida, and Hemichordata. (The set of clade diversity diagrams for the Annelida includes several taxa of questionable affinities which might best be considered *incertae sedis*; these are in the group of diagrams beginning with Cribricyathida and ending with Cornulitidae.) The more diverse marine phyla are represented in Figures 5 to 8. Figure 5 displays orders of marine molluscs; Figure 6 orders of marine arthropods; Figure 7 orders of echinoderms; and Figure 8 orders of marine vertebrates.

The two large phyla of continental animals, the nonmarine Arthropoda and Chordata, are featured in Figures 9 and 10. Nonmarine taxa have been segregated from their marine relatives because we believe that the land and sea are best treated as separate major arenas of evolution (see also Boucot, 1983). Despite the fact that some continental clades contain secondary species which alternate between marine and nonmarine habitats, and that all clades ultimately had their origins in the oceans, the great majority of continental animals evolved *in situ*, isolated from evolutionary activity in the seas. Thus, the segregation of marine and continental taxa enhances assessment of evolutionary patterns within the two arenas as well as comparisons between them. Note that the time axes for the continental clade diversity diagrams in Figures 9 and 10 have been truncated below the Silurian; this is because there is virtually no nonmarine fossil record prior to the mid Paleozoic (see Boucot and Janis, 1983).

The final pair of figures in this chapter (Figures 11 and 12) contains 14 diversity diagrams for families within entire phyla, split again between marine and continental. These diagrams are formatted somewhat differently than in the preceding figures. The spindles have been cut in half and rotated so that the time axis runs horizontally. This arrangement permits easier assessment of the times and magnitudes of diversity change but impedes comparison of changes between groups.

The use of a single level of taxonomic and stratigraphic resolution in all clade diversity diagrams is intended to aid interpretation and comparison of patterns among the various taxa. However, the constancy of resolution does not imply a uniformity of quality throughout the data. The accuracy of the taxonomic and stratigraphic information varies considerably among the taxonomic groups. In general, the quality is much better for marine taxa than for nonmarine taxa. Also, as should be expected, the fossil data are much better (and much more complete) for heavily skeletonized animals than for soft-bodied and lightly sclerotized animals. In fact, many of the diagrams for the latter groups reflect little more than the geologic distribution of Lagerstätten that preserve unusual fossils. This is particularly evident in the long, thin

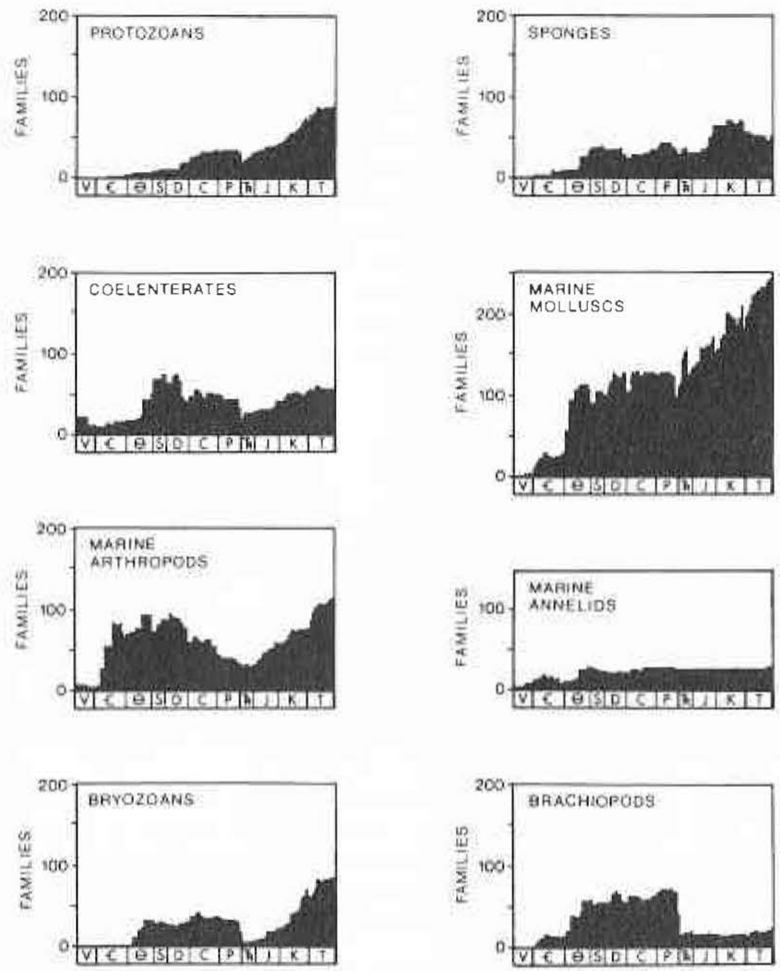


Figure 11. Familial diversity of selected marine animal phyla.

clade diagrams for such extant groups as the Nemertinea and Priapulida (Figure 1); these diagrams show only the extension of stratigraphic ranges from the Recent to the one or more Lagerstätten that happen to contain the groups' early members.

Much of the character of the diversity diagrams for some large clades, such as insects (Figures 2 and 9), also represents the effects of Lagerstätten. For the insects, the more important Lagerstätten include the Upper Carboniferous

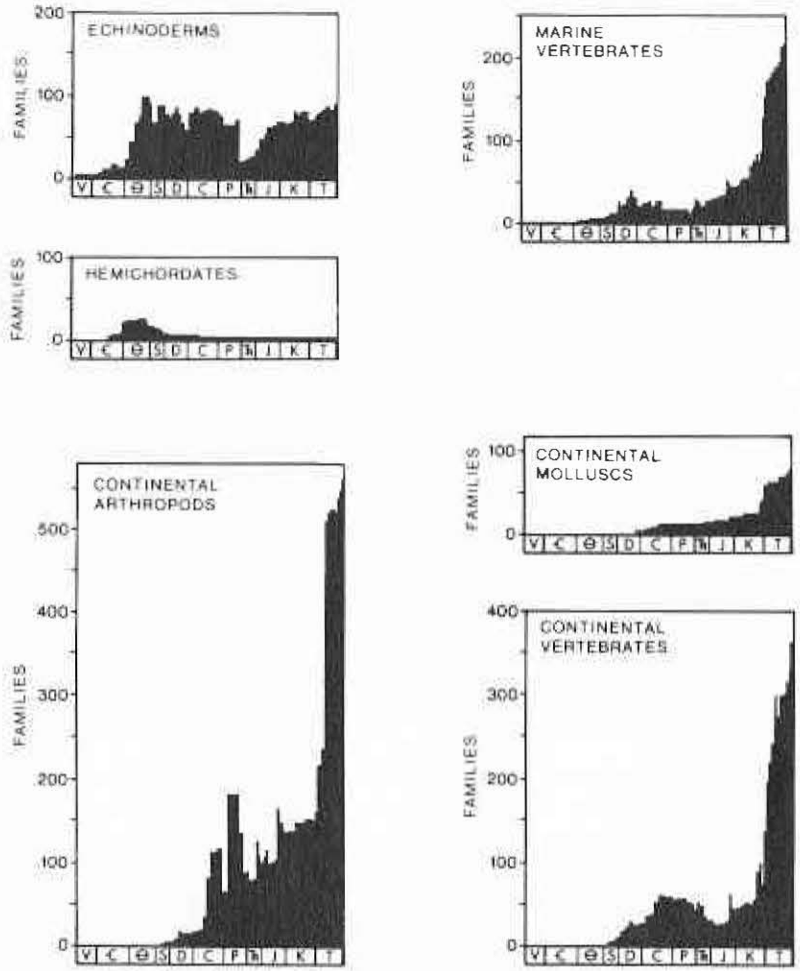


Figure 12. Familial diversity of selected marine and continental animal phyla.

siderite concretion deposits of North America and Europe, the mid-Permian lake deposits of Kansas and Kazakhstan, the Eocene Green River deposits of Wyoming, and especially the Oligocene Baltic Amber of northern Europe. The Baltic Amber alone contributes most of the Cenozoic bulge in the clade diversity diagrams for both insects and other lightly sclerotized terrestrial arthropods (Figures 2, 9, and 12). The effects of Lagerstätten, or of their non-occurrence, are even seen in some well-skeletonized groups with fairly

extensive fossil records. The drop in the diversity of continental vertebrates in the Jurassic (Figure 12), for example, probably reflects largely a paucity of fossiliferous continental deposits between the Rhaetian and Tithonian (see also Carroll, 1977; Padian and Clemens, 1985, this volume).

These shortcomings of the fossil record, along with the problems associated with family-level data and 5 to 10 myr-long stages, do limit the value of the clade diversity diagrams presented here. However, we believe that a great deal still can be learned from them about the shape of evolution—about the success and failure of taxa and about the apparent order, or disorder, in their radiations and extinctions. Thus, we hope that this "atlas" will aid in the assessment and interpretation of evolutionary history as well as serve as a baseline for the compilation of more accurate and detailed diversity data.

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